

Two New Brittle Star Species of the Genus *Ophiothrix* (Echinodermata: Ophiuroidea: Ophiotrichidae) from Coral Reefs in the Southern Caribbean Sea, with Notes on Their Biology

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ABSTRACT.—Two new species, *Ophiothrix stri* and *Ophiothrix cimar*, inhabit shallow reef-platforms and slopes in the Southern Caribbean, and occur together at localities in Costa Rica and Panama, nearly to Colombia. What appears to be an undescribed species resembling *O. cimar* has been reported from eastern Venezuela. In recent years, reefs where the species were previously observed have deteriorated because of environmental degradation. As a consequence, populations of the new species may have been reduced or eradicated. The new species have previously been mistaken for *O. angulata*, *O. brachyactis*, and *O. lineata*. *Ophiothrix lineata*, *O. stri*, and *O. cimar* have in common a suite of morphological features pointing to their systematic affinity, and a similar pigmentation pattern consisting of a thin, dark, medial arm stripe flanked by two pale stripes. *Ophiothrix lineata* is similar to Indo-Pacific members of the subgenus *Placophiothrix* and closely resembles *Ophiothrix stri*. The latter is extremely similar to *O. synoecina*, from Colombia, and both can live in association with the rock-boring echinoid *Echinometra lucunter*. Although *O. synoecina* is a protandric hermaphrodite that reportedly broods its young externally, the new species are gonochoric and do not brood. Their eggs are of a size indicative of abbreviated larval development, and the gametes of *O. stri* produce demersal embryos that develop within a large, adhesive fertilization envelope. The new species and related forms may belong to one of several clades containing shallow-water Caribbean *Ophiothrix* species with abbreviated development and relatively restricted larval dispersal.

KEYWORDS.—Abbreviated demersal development, brooding, *Comactinia*, *Echinometra*, *Placophiothrix*

INTRODUCTION

The brittle stars of the family Ophiotrichidae are readily distinguished by the stumps, spines, and spinelets on their disks, their long, thorny arm spines, and an oral armament consisting solely of dental papillae. However, the distinctions among genera within the family are problematical, and the identification of ophiotrichids has been a continuing "source of considerable trouble to systematists owing to the great variability of many of the species" (A. M. Clark 1966:637). Due to their abundance and ubiquity in shallow, warm-water marine habitats, ophiotrichids in the genus *Ophiothrix* have been studied in nature and the laboratory by biologists in various disciplines. The brilliant colors of some species, and their association with attractive corals and sponges, have consistently

drawn the attention of underwater photographers. Therefore, frustration created by the unsettled taxonomy of ophiotrichids is felt not only by systematists.

The confusion engendered by ophiotrichid taxonomy is a long-standing problem in the Caribbean region where the common *Ophiothrix* species are extremely variable, and the variability of the very rare species has not been characterized (Hendler et al. 1995). Under the circumstances, it is not surprising that the occurrence of some *Ophiothrix* species, even accessible widespread species, has gone undetected. In the present contribution, two such new species of *Ophiothrix* are described, which live on coral reefs from Costa Rica to Colombia. They were most recently observed and collected in Bocas del Toro Province, Panama, at sites that are relatively unaffected by the regional deterioration of coral reefs

(Guzmán and Guevara 1998a, b, 1999). However, it is not known if both species still survive at severely impacted sites where they occurred in previous decades. Their populations may have been reduced or eradicated during the decline of coral reefs that is manifested throughout the Caribbean, largely as a consequence of human-caused environmental change (Gardner et al. 2003; Birkeland 2004).

In the vicinity of Panamanian reefs near Galeta, and in the San Blas Islands where I found both of the new species in the 1970s, there have been several destructive oil spills, and declines in coral cover attributed to coral bleaching, coral mining, and unplanned coastal development (Birkeland et al. 1976; Guzmán et al. 1994; Guzmán 2003). At Cahuita National Park, Costa Rica, where I collected them in the 1980s, the reef was subsequently damaged by coastal uplift triggered by an earthquake, and by the impact of siltation and other anthropogenic stressors (Cortés and Risk 1985; Cortés et al. 1993; Fonseca 2003). The situation at Caledonia Bay, where the species were first collected in the 1930s, has not since been reported (Garth 1945), but the condition of the reefs has probably deteriorated there, as it has elsewhere in Panama (Guzmán 2003).

The similarity of the new species to each other, and to congeners including the highly variable *Ophiothrix angulata* (Say, 1825), has hampered their recognition and study. Therefore, my objective is to facilitate their identification. For the same reason, I also refer to what may be another similar, undescribed species from Venezuela (Zoppi de Roa 1967). A further aim is to report on some significant aspects of their reproduction and ecology, and their relationship to other species of *Ophiothrix*.

MATERIALS AND METHODS

Initial studies and collections were done in the vicinity of the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute (STRI), from 1971 to 1975. However, the present contribution is largely based on observations and collections gathered in 2003 during a regional

survey sponsored by the STRI's Bocas Research Station, and in 1986 and 1987 at nearby Costa Rican localities during a study of Cahuita National Park. The results are also derived from specimens of the Allan Hancock Foundation Pacific Expeditions deposited in the Natural History Museum of Los Angeles County (LACM). Type specimens of related species from the echinoderm collections of the Museum of Comparative Zoology of Harvard University (MCZ) and the National Museum of Natural History of the Smithsonian Institution (USNM) were compared as well.

Living and preserved specimens were examined with a stereomicroscope and measured with a calibrated ocular micrometer, calipers, or millimeter ruler, as necessary. Animals were anesthetized using magnesium chloride or Epsom salts solutions prior to preservation in ethanol, and some specimens were dried. Descriptive statistics are based exclusively on alcohol-preserved animals. To prepare skeleton structures for scanning electron microscopy, soft tissue was removed from alcohol-preserved material using dilute sodium hypochlorite solution, and the specimen was washed in water and air-dried prior to sputter coating. The terminology employed for morphological characters follows Hender et al. (1995). Color patterns running the length of the arm are referred to as stripes; those running across the arm are called bands. Abbreviations used are dd (disk diameter) and AL (arm length). Type specimens of the new species are deposited at the LACM, USNM, and Museo de Zoología of the Universidad de Costa Rica (UCR).

SYSTEMATIC ACCOUNT

Family Ophiotrichidae Ljungman, 1867

Genus *Ophiothrix* Müller and Troschel, 1840

Ophiothrix cimar, **new species**

FIGURE 1A-F

Holotype.—COSTA RICA, LIMON PROV.: (LACM 1987-68.3), Sta. CR 87-31, 24 May 1987, 9°44.97' N, 82°49.3' W, NE of Sloth River mouth, 0-1 m, coll. G. Hender and R. W. Peck.

Paratypes.—COSTA RICA, LIMON PROV.: (LACM 1986-106.2), 8 alc, Sta. CRA 86-1, 26 Jul. 1986, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler; (LACM 1986-115.1), 1 alc, Sta. CRA 86-8, 27 Jul. 1986, 9°37.9' N, 82°36.97' W, off Punta Mona (Punta Carreta), 6-15 m, coll. G. Hendler; (LACM 1986-137.1), 1 alc, Sta. CRA 86-23, 28 Jul. 1986, 9° 44.18' N, 82° 48.6' W, Punta Cahuita Reef, 2-9 m, coll. G. Hendler; (LACM 1986-141.2), 1 alc, Sta. CRA 86-27, 29 Jul. 1986, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 2-6 m, coll. G. Hendler; (LACM 1986-154.2), 3 alc, Sta. CRA 86-37, 31 Jul. 1986, 9°39.7' N, 82°45.53' W, off Puerto Viejo, 1-4 m, coll. G. Hendler; (LACM 1986-197.2), 1 alc, 29 Oct. 1986, 9°44.18' N, 82°48.7' W, Punta Cahuita Reef, 1-5 m, coll. R. C. Brusca and P. M. Delaney; (LACM 1987-40.1), 8 alc, Sta. CR 87-1, 19 May 1987, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 1-2 m, coll. G. Hendler and R. W. Peck; (LACM 1987-43.1), 6 alc, Sta. CR 87-4, 19 May 1987, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (LACM 1987-67.6), 1 dry, Sta. CR 87-4, 19 May 1987, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (LACM 1987-43.3), 2 SEM, Sta. CR 87-4, 19 May 1987, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (LACM 1987-50.2), 1 alc, Sta. CR 87-12, 20 May 1987, 9°44.53' N, 82°48.55' W, Punta Cahuita Reef, 2-3 m, coll. G. Hendler and R. W. Peck; (USNM 1073475), 1 alc, Sta. CR 87-13, 20 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (UCR-467), 1 alc, Sta. CR 87-13, 20 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (LACM 1987-63.2), 6 alc, Sta. CR 87-25, 23 May 1987, 9°43.95' N, 82° 48' W, Punta Cahuita Reef, 3-15 m, coll. G. Hendler and R. W. Peck; (LACM 1987-66.1), 1 alc, Sta. CR 87-28, 23 May 1987, 9°44.7' N, 82°48.68' W, Punta Cahuita Reef, 1 m, coll. G. Hendler, R. W. Peck; (LACM 1987-67.1), 8 alc, Sta. CR 87-29, 87-30, 23 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-2 m, coll. G. Hendler and R. W. Peck; (LACM 1987-67.5), 2 alc, Sta. CR 87-29, 87-30, 23 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-2 m, coll. G. Hendler and R. W. Peck; (LACM 1987-68.2), 1 alc, Sta. CR 87-31, 24 May 1987, 9°44.97' N, 82°49.3' W, NE of Sloth River mouth, 0-1 m, coll. G. Hendler and R. W. Peck. PANAMA, BOCAS DEL TORO PROV.: (LACM 2003-51.6), 1 alc, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82 ° 10.33', Wild Cane Key, N. Bastimentos Id., 0.9-4.2 m, coll. G. Hendler et al.; (LACM 2003-64.3), 1 alc, Sta. BDT 03-16, 7 Aug. 2003, 9°27.2' N, 82°18.02' W, S. Swan Key, 3 m, coll. G. Hendler et al.; (LACM 2003-65.3), 1 alc, Sta. BDT 03-17, 7 Aug. 2003, 9°25.6' N, 82°19.5' W, Boca del Drago, N. W. Colon Id., 4.5 m, coll. G. Hendler et al. PANAMA, COLON PROV.: (LACM 1939-181.3), 1 dry, Sta. AHF A8-39, R/V Velero III, 4 Apr. 1939, 8°53.72' N, 77°41.4' W, Bahía Caledonia, off San Fulgencio Pt., shore; (LACM 1939-217.4), 2 dry, Sta. AHF A50-39, R/V Velero III, 26 Apr. 1939, 8°53.63' N, 77°41.4' W, Bahía Caledonia, off San Fulgencio Pt., shore; (LACM 1939-222.3), 4 dry, Sta. AHF A57-39, R/V Velero III, 27 Apr. 1939, 8°53.72' N, 77°41.5' W, Bahía Caledonia, off San Fulgencio Pt., shore; (LACM 1971-671.1), 2 dry, 3 Apr. 1971, 9°24.3' N, 79°51.9' W, Punta Galeta, 0.3-0.6 m, coll. G. Hendler; (LACM 1971-672.1), 2 dry, 1-8 Apr. 1971, 9°24.3' N, 79°51.9' W, Punta Galeta, coll. G. Hendler; (LACM 1974-248.1), 2 dry, 30 Oct. 1974, 9°24.05' N, 79°51.1' W, Largo Remo Key, 0.3-0.6 m, coll. G. Hendler; (LACM 1974-250.1), 4 dry, 30 Nov. 1974, 9°24.3' N, 79°51.9' W, Punta Galeta, 6-10.6 m, coll. G. Hendler; (LACM 1974-252.1), 5 dry, 24 Aug. 1974, 9°24.3' N, 79°51.9' W, Punta Galeta, 0-1 m, coll. G. Hendler; (LACM 1974-253.1), 1 dry, 14 Dec. 1974, 9°24.3' N, 79°51.9' W, Punta Galeta, coll. G. Hendler; (LACM 1975-704.1), 1 dry, 26 Jan. 1975, 9°33.7' N, 79°41' W, Iron Castle Pt., Portobello, 0.9-3 m, coll. G. Hendler; (LACM 1977-305.1), 12 alc, 1-30 Nov. 1977, 9°24.3' N, 79°51.9' W, Punta Galeta, coll. K. Dunlap.

Etymology.—The species was studied, in part, under the auspices of the Centro de Investigaciones en Ciencias del Mar y Limnología, of the Universidad de Costa Rica.

The specific name is based on the acronym for that organization, CIMAR.

Description.—Disk diameter of holotype 9.3 mm, length of longest arm 58 mm. Specimens examined ranged from 3.3-11.3 mm dd, and from 18-65 mm AL. AL/dd ratios ranged from 4.4-8.5 (\bar{X} = 5.9, SE = 0.12, n = 49).

Disk typically pentagonal, somewhat inflated, interradii protruding between arms; spent individuals with little gonadal tissue have round disks (Fig. 1A, B). Scales moderately large, rounded, tessellate, partially obscured by integument. Spines on disk evenly spaced, somewhat tapering, rugose, short (approximately 1 mm tall), largest between radial shields; generally no more than 1 spine borne on a scale; spines distributed in 1-2 irregular rows between radial shields, in approximately 5 irregular interradii rows; usually a few spinules on dorso-medial portion of interradius and radial shield. Radial shields flat, length approximately one-third dd; subtriangular, with thickened, concave adradial edge, abradial edge almost straight, distal edge concave, sometimes strongly so; corners forming rounded lobes; adradial corners in contact, extending beyond disk and over arm base (Fig. 1C).

Jaw with small, peg-shaped dental papillae on ventral apex, larger papillae on lateral edges, surrounding several shorter, thicker papillae, separated from teeth by several pairs of larger, bar-shaped, obliquely set dental papillae (Fig. 1F). Oral shield subtriangular, centrally depressed, with slightly concave lateral sides, long convex distal edge, rounded corners. Madreporite larger than oral shield, more irregularly proportioned, sometimes with pore at distal edge. Adoral shield proximal to oral shield and half its size, subtriangular, somewhat inflated. Ventral interradius naked, with long bursal slits buttressed by pair of small, flared ossicles distal to oral shield and large, flared genital scales.

Arms somewhat dorso-ventrally compressed in appearance due to long, horizontally projecting lateral arm spines; in cross section dorsal surface somewhat convex, ventral surface flat. Arm breadth flaring at about one-half to one dd beyond disk

edge, due to presence of longest arm spines at that position; thereafter tapering gradually toward arm tip. Dorsal arm plates rhombic, somewhat convex or keeled; wider than long, with concave proximal edges, convex distal edges; distal edge markedly thickened, upper surface of plate with small, slightly inflated proximal and distal medial protrusions (Fig. 1D). Adjacent dorsal plates in contact or nearly so; several plates nearest disk markedly reduced in size, barely contiguous, not in contact with disk; basal lateral arm plates and spines on opposite sides of arm in close contact. Surface of dorsal arm plate of dried specimens appearing granulose under low magnification.

Lateral arm plate with prominent ridge bearing up to 10 slender arm spines; spine length increasing markedly from dorsal-most to fourth spine, then decreasing stepwise to ventral-most spine. Length of longest spine approximately 2.5-3 times width of dorsal arm plate. Dorsal spines at base of arm rounded in cross-section, rugose, slender, gradually tapering from base; shaft of more distal dorsal spines dorso-ventrally compressed (Fig. 1C, D). Ventral spines, particularly longest spine, dorso-ventrally compressed, with slight distal bend; lateral edges aciculate, distal tip somewhat flared (Fig. 1E). Dorsal-most spines directed somewhat dorsally; spines beneath disk short, directed posteriorly; ventral-most spines on distal one-third to one-half of arm very small, with hyaline terminal hook and several subterminal teeth. Tentacle scale single, embedded in integument, minute, flat to granular, with distal point (Fig. 1E).

First ventral arm plate in mouth angle with medial slot separating 2 proximally directed points; 2-3 most basal plates centrally depressed, overlapping, longer than wide, centrally depressed (Fig. 1F). Remaining plates approximately twice as wide as long, nearly touching, narrow, constricted medially; lateral edges convex, concave proximal and distal edges of adjacent plates bridged by band of soft tissue approximately one-half as long as plate (narrower in dry specimens), obscuring proximal portion of plate.

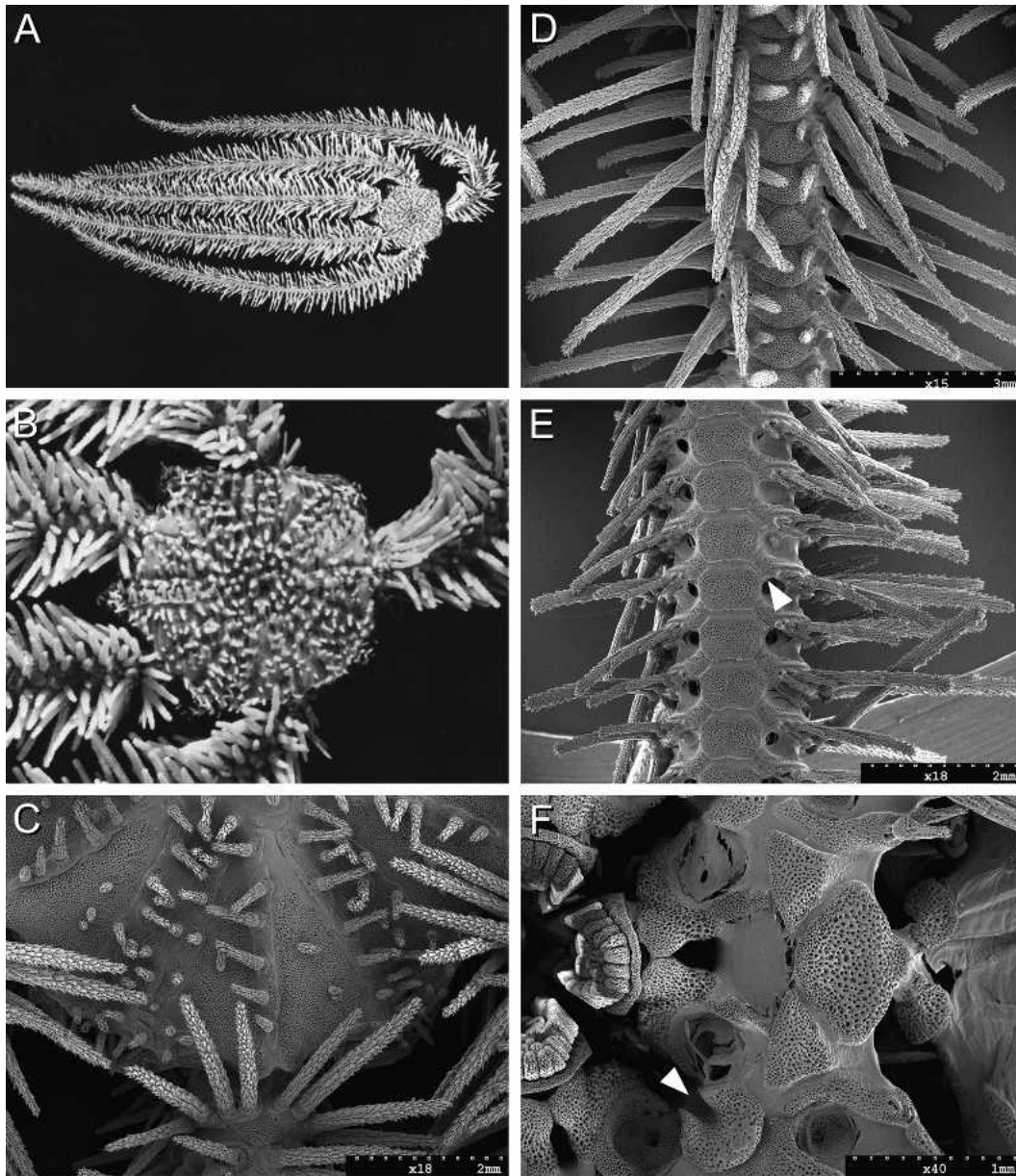


FIG. 1. *Ophiothrix cimar*. A-B, photomicrographs of dried paratype, disk diameter = 7.7 mm (LACM 1987-67.6); C-F, scanning electron micrographs of paratypes (LACM 1987-43.3), treated to remove integument. A, entire, dorsal view; B, disk and base of arms, dorsal view; C, Disk edge showing few spines on radial shields, gap between disk and arm, and rugose, cylindrical spines on dorsal surface of arms and disk; D, arm, dorsal view; E, arm, ventral view, with tentacle scale indicated by arrowhead; F, Detail of oral frame, ventral view, showing structures associated with jaw including deeply incised 1st ventral arm plate (arrowhead).

Living individuals brown, pinkish-brown, reddish-brown, grayish-brown, blackish, or yellowish. Arm color usually contrasts with disk, and arm spines differ-

ently colored, frequently paler, rarely darker, than dorsal surface of arm. Disk spines often whitish, yellowish or reddish, usually contrasting in coloration with

darker radial shields. Interradial coloration generally contrasts with dorsal surface of disk; pale colored gonads sometimes visible through naked interradian integument. Arms have thin, dark, medial dorsal stripe flanked by paler stripes; arms also banded dorsally and ventrally, with about every fourth segment more darkly pigmented than the others. Ventral arm plates and oral frame with dark brown flecks and pale grayish-brown and reddish-brown blotches that may cover a portion or almost entire plate, surrounded by pale pigmentation. Tube feet yellowish; oral tentacles pale yellowish-brown.

Preserved specimens with disk grayish, purplish-gray, purplish-brown, or brownish-gray; large ossicles such as radial shields and ventral arm plates often marked with a combination of dark, moderately dark and pale colors; patches of white at the base of some disk spines and at edges of radial shields; black patches on some scales; some specimens with microscopic network of black and pale markings between disk scales. Disk spines pale brown. Ventral interradius dark brown to black sometimes mottled with yellowish-brown. Arms retain pattern of the stripes and bands visible in living individuals. Oral tentacles white with black flecks, or grayish.

Variations.—Juveniles differ from adults in several respects. An individual 3.3 mm dd has typical disk spines, but bare radial shields. The arm spines are slender, somewhat dorso-ventrally compressed, lacking flared tip; the largest are slightly rugose. Its primary plates are irregular, but in a 4.4 mm individual a central and 5 radial plates are evident.

Comparisons.—*Ophiothrix cimar* is notably similar to *Ophiothrix lineata* Lyman, 1860. Both have a somewhat dorso-ventrally compressed body shape, large fairly bare radial shields, and a similar pattern of arm stripes. However, continuation of the dark and pale arm stripes onto the disk between the radial shields, which is marked in adult *O. lineata*, is only noticeable in very small individuals of *O. cimar*. Ventral arm bands are more noticeable in *O. cimar* than in *O. lineata*. *Ophiothrix cimar* is a smaller species,

with maximum AL of 58 mm and up to 8.5 times the dd, compared with the 120 mm arms, 10 times the dd, found in *O. lineata*. It is distinguished by spines on the disk, rather than sparse, minute stumps. Moreover, it is cryptic and lives in hard substrate, whereas *O. lineata* is a symbiont of tube sponges (Hendler 1984). The dorso-ventrally compressed body shape of *O. cimar* somewhat resembles that of *O. stri*, *O. brachyactis* H. L. Clark, 1915, and *O. hartfordi* A. H. Clark, 1939, but it is reliably distinguished by the spinose disk.

An *Ophiothrix* species from eastern Venezuela, identified by Zoppi de Roa (1967) as *Ophiothrix brachyactis*, has a spinose disk like that of *O. cimar* rather than a granulose disk like the holotype of *O. brachyactis*. Its disk morphology, banded arms, and laterally directed arm spines also resemble the features of *O. cimar*. However, the arms lack a dark medial stripe and are only 2-3 times as long as the dd (see Zoppi de Roa 1967: fig. 20). Moreover, it lives in masses of mussels and algae, and thus appear to occupy a different microhabitat than *O. cimar*. The available evidence indicates a similarity of the Venezuelan specimens to *O. cimar*, but suggests that it represents an undescribed species.

Distribution.—At present, known from Cahuita, Costa Rica to Caledonia Bay, Panama, and from the intertidal to a depth of approximately 10 m, generally in less than 3 m.

Biology.—Individuals are cryptic, and were found beneath coral rubble, including large slabs of *Acropora palmata*, and at least sometimes in close proximity to encrusting sponge. When disturbed, they initiated a vigorous escape response. Individuals typically accumulated clumps of flocculent, mucus-bound silt on the disk and arm spines, unlike sympatric *O. angulata* and *O. stri*. The species is restricted to shallow water near fringing coral reef, and generally occupies rubble-strewn back reef habitats with varying degrees of coral cover and three-dimensional relief. Some individuals were found on fairly high-energy reef platform, as well as under much more protected conditions beneath coral rubble in a *Thalassia* bed.

All of the specimens of *O. cimar* were examined externally for evidence of brooding, and embryos were not seen in the bursal slits, or in the bursae of dissected females. Of the 20 specimens that were dissected, 12 were male (\bar{X} = 7.89 mm dd, SE = 0.51, range = 4.79-10.51), and eight were female (\bar{X} = 9.11 mm dd, SE = 0.47, range = 6.92-11.31). The overlapping sizes of males and females, and the lack of hermaphroditic specimens, indicate that the species is gonochoric. The eggs in gonads of 5 of the larger alcohol-preserved females (\bar{X} = 9.87 mm dd, SE = 0.43, range = 9.04-11.31) were whitish, and had a mean diameter of 0.16 mm (SE = 0.002, n = 50, range = 0.128-0.208).

Ophiothrix stri, new species

FIGURE 2A-F.

Holotype.—PANAMA, BOCAS DEL TORO PROV.: (LACM 2003-51.2), Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82° 0.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.

Paratypes.—COSTA RICA, LIMON PROV.: (LACM 1986-106.1), 3 alc, Sta. CRA 86-1, 26 Jul. 1986, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler; (LACM 1986-121.1), 1 alc, Sta. CRA 86-12, 27 Jul. 1986, 9°40.8' N, 82°45.53' W, N of Puerto Viejo, 1-3 m, coll. G. Hendler; (LACM 1986-127.1), 1 alc, Sta. CRA 86-18, 27 Jul. 1986, 9°40.8' N, 82°45.53' W, N of Puerto Viejo, 1-3 m, coll. G. Hendler; (LACM 1986-136.1), 6 alc, Sta. CRA 86-22, 28 Jul. 1986, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 2-9 m, coll. G. Hendler; (LACM 1986-139.1), 1 alc, Sta. CRA 86-25, 28 Jul. 1986, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 2-9 m, coll. G. Hendler; (LACM 1986-141.1), 3 alc, Sta. CRA 86-27, 29 Jul. 1986, 9°44.18' N, 82°48.6' W, Punta Cahuita Reef, 2-6 m, coll. G. Hendler; (LACM 1986-154.1), 5 alc, Sta. CRA 86-37, 31 Jul. 1986, 9°39.7' N, 82°45.53' W, off Puerto Viejo, 1-4 m, coll. G. Hendler; (UCR-468), 3 alc, 29 Oct. 1986, 9°44.18' N, 82°48.7' W, Punta Cahuita Reef, 1-5 m, coll. R. C. Brusca, and P. M. Delaney; (LACM 1987-49.1), 4 alc, Sta. CR 87-11, 20 May 1987,

9°44.53' N, 82°48.55' W, Punta Cahuita Reef, 1-2 m, coll. G. Hendler, and R. W. Peck; (LACM 1987-50.1), 1 alc, Sta. CR 87-12, 20 May 1987, 9°44.53' N, 82°48.55' W, Punta Cahuita Reef, 2-3 m, coll. G. Hendler, R. W. Peck; (LACM 1987-51.1), 1 alc, Sta. CR 87-13, 20 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (LACM 1987-51.4), 6 alc, Sta. CR 87-13, 20 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-3 m, coll. G. Hendler and R. W. Peck; (LACM 1987-63.1), 3 alc, Sta. CR 87-25, 23 May 1987, 9°43.95' N, 82°48' W, Punta Cahuita Reef, 3-15 m, coll. G. Hendler, and R. W. Peck; (LACM 1987-67.4), 11 alc, Sta. CR 87-29, 87-30, 23 May 1987, 9°44.37' N, 82°48.7' W, Punta Cahuita Reef, 1-2 m, coll. G. Hendler, and R. W. Peck; (LACM 1987-68.1), 1 alc, Sta. CR 87-31, 24 May 1987, 9°44.97' N, 82°49.3' W, NE of Sloth River mouth, 0-1 m, coll. G. Hendler and R. W. Peck. PANAMA, BOCAS DEL TORO PROV.: (LACM 2003-105.1), 2 alc, 12 Aug. 2003, 9°27.17' N, 82°18.01' W, Swan Cay, 1.5 m, coll. K. Fitzhugh and W. G. Keel; (LACM 2003-51.1), 18 alc, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82°10.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.; (LACM 2003-51.4), 2 alc, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82° 10.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.; (LACM 2003-51.5), 25 alc, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82° 10.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.; (USNM 1073476), 2 alc, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82°10.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.; (LACM 2003-51.8), 2 SEM, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82°10.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.; (LACM 2003-51.7), 1 dry, Sta. BDT 03-4, 4 Aug. 2003, 9°20.66' N, 82°10.33' W, Wild Cane Key, N. Bastimento Id., 0.9-4.2 m, coll. G. Hendler et al.; (LACM 2003-64.1), 3 alc, Sta. BDT 03-16, 7 Aug. 2003, 9°27.2' N, 82°18.02' W, S. Swan Key, 3 m, coll. G. Hendler et al.; (LACM 2003-64.2), 3 alc, Sta. BDT 03-16, 7 Aug. 2003, 9°27.2' N, 82°18.02' W, S. Swan Key, 3 m, coll. G. Hendler et al.; (LACM 2003-64.6), 1 alc, Sta.

BDT 03-16, 7 Aug. 2003, 9°27.2' N, 82°18.02' W, S. Swan Key, 3 m, coll. G. Hendler et al.; (LACM 2003-65.2), 2 alc, Sta. BDT 03-17, 7 Aug. 2003, 9°25.6' N, 82°19.5' W, Boca del Drago, N.W. Colon Id., 4.5 m, coll. G. Hendler et al. PANAMA, COLON PROV: (LACM 1939-174.2), 1 dry, Sta. AHF A1-39, R/V Velero III, 3 Apr. 1939, 8°53.7' N, 77°40.5' W, Bahia Caledonia, islet south of Isla de Oro, shore; (LACM 1939-222.4), 1 dry, Sta. AHF A57-39, R/V Velero III, 27 Apr. 1939, 8°53.72' N, 77°41.5' W, Bahia Caledonia, off San Fulgencio Pt., shore; (LACM 1974-249.1), 3 dry, 15 Dec. 1974, ca. 9°33.7' N, 79°41' W, Iron Castle Point, Portobello, 0-3 m, coll. G. Hendler; (LACM 1974-250.2), 4 dry, 30 Nov. 1974, 9°24.3' N, 79°51.9' W, Punta Galeta, 6-10.6 m, coll. G. Hendler; (LACM 1974-251.1), 1 dry, 2 Sep. 1974, 9°24.3' N, 79°51.9' W, Punta Galeta, 0-10.6 m, coll. G. Hendler; (LACM 1974-254.1), 1 dry, 25 Nov. 1974, ca. 9°33.7' N, 79°41' W, Iron Castle Pt., Portobello, 0-1.5 m, coll. G. Hendler; (LACM 1975-705.1), 1 dry, 18 Apr. 1975, ca. 9°33.7' N, 79°41' W, Iron Castle Pt., Portobello, 0.9-3 m, coll. G. Hendler; (LACM 1975-706.1), 1 dry, 25 Mar. 1975, ca. 9°32.75' N, 78° 54.5' W, Media Tupo, San Blas, 0.9-1.5 m, coll. G. Hendler; (LACM 1975-707.1), 4 dry, 25 Mar. 1975, ca. 9°30.75' N, 78°47.83' W, Salar Salar, 6 m, coll. G. Hendler; (LACM 1975-708.1), 4 dry, 26 Mar. 1975, ca. 9°30.75' N, 78°47.83' W, Salar Salar, 1.5 m, coll. G. Hendler.

Etymology.—The species was studied, in part, under the auspices of the Smithsonian Tropical Research Institute. The specific name is based on the acronym for that organization, STRI.

Description.—Disk diameter of holotype 9.8 mm, length of longest arm 42 mm. Specimens examined range from 2.3-10.6 mm dd, and from 8.6-54 mm AL. AL/dd ratios ranged from 2.8-7.2 (\bar{X} = 5.0, SE = 0.08, n = 91).

Disk generally round, not inflated, dorsal margin sharply demarcated from naked ventral interradius; interradii protruding in ripe individuals (Fig. 2A, B). Scales moderately large, rounded, tessellate, partially obscured by integument, bearing prominent stumps. Stumps numerous, nearly as wide as tall (approximately 0.2 mm), with

hemispherical tip bearing approximately 20 microscopic thorns; generally only 1 stump borne on a scale; stumps distributed in 1-2 irregular radial rows, 4-5 irregular interradii rows; interradii rows protruding slightly between arms; a dense group of stumps at disk edge capping distal lobe of radial shield; only rarely are a few granules on lateral edge of interradius. Radial shields subtriangular, approximately one-third dd in length, with slightly concave adradial edge, concave distal edge, straight to slightly convex abradial edge; corners forming rounded lobes; central portion of plate slightly inflated; bearing several small granules, generally near abradial edge; adradial corners separated by several small ossicles in series with dorsal arm plates, bridging gap between arm and disk edge. Surface of radial shields and dorsal arm plates of dried specimens appearing granulate under low magnification (Fig. 2C).

Jaw with short, peg-shaped dental papillae on ventral apex, larger papillae on lateral edges surrounding inner series of shorter papillae, separated from teeth by several chevrons of large, bar-shaped, obliquely set dental papillae (Fig. 2F). Oral shield subtriangular to subpentagonal, centrally depressed, with straight or somewhat concave lateral edges, long convex distal edge, rounded corners. Madreporite larger, more rounded or lobate than oral shield, sometimes with 1-2 microscopic pores near concave distal edge. Adoral shield proximal to oral shield and one-half its size, subtriangular, somewhat inflated. Ventral interradius naked, with long bursal slits buttressed by pair of ossicles distal to oral shield, and with large, flared genital scales.

Arm compressed in appearance due to horizontal orientation of arm spines; in cross section dorsal surface slightly convex, ventral surface flat. Arm breadth flaring at less than 1 dd beyond disk edge, due to presence of longest arm spines and widest dorsal arm plates at that position; thereafter tapering gradually toward arm tip. Dorsal arm plates thick, generally flat or slightly rounded, not keeled; successive plates closely abutting, in contact for about one-third width of plate (Fig. 2D). Plates sub-

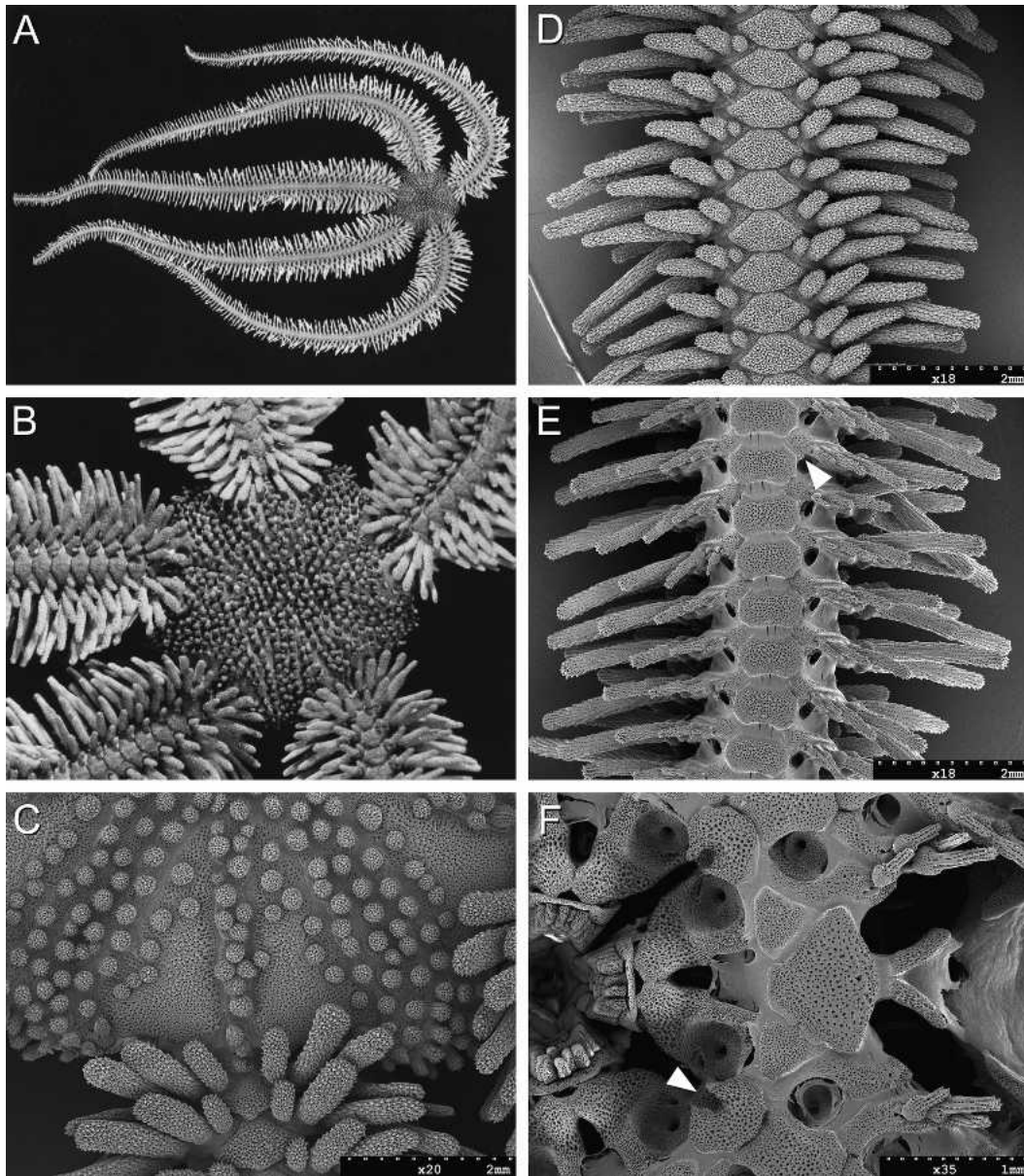


FIG. 2. *Ophiothrix stri*. A-B, photomicrographs of dried paratype, disk diameter = 8.0 mm (LACM 2003-51.7); C-F, scanning electron micrographs of paratypes (LACM 2003-51.8), treated to remove integument. A, entire, dorsal view; B, disk and base of arms, dorsal view; C, Disk edge showing few rounded stumps on radial shields, series of small ossicles connecting disk and arm, and rugose, compressed, proximally directed spines on base of arm; D, arm, dorsal view; E, arm, ventral view, with tentacle scale indicated by arrowhead; F, Detail of oral frame, ventral view, showing structures associated with jaw including deeply incised 1st ventral arm plate (arrowhead).

hexagonal, twice as wide as long; proximal and distal edges straight, proximo-lateral edges concave; 3 disto-lateral edges convex, but sometimes merging into single convex

shape. Small, basal dorsal arm plates differ in having medial protrusion on distal edge; first plate overlaps the second and is overlapped by lateral arm plates.

Lateral arm plates with prominent ridge bearing up to ten arm spines; dorsal and ventral spines conspicuously different. Spine length increasing markedly from dorsal-most to fourth spine, then decreasing gradually to ventral-most spine. Length of longest spine approximately 1.3 times width of dorsal arm plate. Dorsal-most spine only 1-4 times longer than wide, ovoid. Dorsal spines on first free joint directed toward disk, those on distal joints directed laterally in horizontal plane of arm (Fig. 2C). On basal joints dorsal-most three spines thick, rugose; shaft distinctly ovoid in cross section; broad, distal portion somewhat dorso-ventrally compressed, tapering to blunt point (Fig. 2C, D). Lower spines narrow, with slight distal bend, shaft dorso-ventrally compressed, lateral edges aciculate (Fig. 2E). Space between spines on adjacent basal joints constricted due to large diameter of dorsal spine; distance between slender spines on distal joints exceeding spine diameter. Ventral-most spines on distal one-half to two-thirds of arm very small, with hyaline terminal hook and 1-3 subterminal teeth. Tentacle scale single, minute, embedded in integument, granular to flat, triangular with distal point (Fig. 2E).

First ventral arm plate in mouth angle with medial slot separating 2 proximally directed points; following plate longer than wide, centrally depressed, overlapping 3rd plate, which is also centrally depressed (Fig. 2F). Remaining plates very short, broad, octagonal; 5 proximal edges nearly straight, 3 distal edges straight or concave; successive plates separated by straight, broad ribbons of soft tissue nearly one-third width of plate.

Living individuals purplish-red, purplish-brown, pale grayish purple-brown, ochre, or yellow; ventral surface pinkish. Disk may be grayish brown or purple with black interradii, arm spines grayish-brown; arms brownish-gray, brown, or grayish-purple with black, dark brown, orange, or reddish medial stripe flanked by tan or salmon-colored stripes. Stripes indistinguishable in intensely dark individuals, except near tips of arms. Arm bands particularly evident in small or pale-colored

individuals; 2-3 pale arm joints alternate with each darker joint. Ventral surface of arms whitish, pale purple or pinkish, with broad brown medial stripe which is nearly imperceptible in deeply pigmented individuals; oral frame whitish with flecks of darker color; ventral interradii deep purple or brown, partially whitish in ripe individuals; oral tentacle and first tube feet pale yellowish; tube feet gray with black flecks, oral tentacles yellowish with brown tip.

In darkly-pigmented, preserved specimens, disk dark purplish-gray and black; arms with thin, blackish medial stripe flanked by pale stripes. Arm spines gray with black flecks, contrasting with arms. Lateral arm plates and ventral arm plates with mottled black pattern forming microscopic white bands near distal edge of lateral arm ridge. Oral region whitish to pale grayish-violet, with black patches and flecks on major ossicles. Ventral interradius dark blackish-purple and brown. Ventral arm surface pale brownish-gray or violet-gray, with microscopic black flecks and broad dark medial stripe. Tube feet black with pale papillae. Small individuals relatively pale. Yellow individuals with arm spines and median arm stripe brown.

Variations.—A juvenile individual 2.3 mm dd, has a central plate covering 25% of the dd, and the radial plates are very small and separated by intercalary scales. Disk armament consists of multifid spinules with a thick shaft; 0-1 per scale and several per radial shield. The arm spines are compressed, and basal spines are wide, with strongly aciculate lateral edges. The central plate covers 10% of the dd in a 3.1 mm dd individual, 6% in a 6.7 mm individual, and is often indiscernible in large specimens. The 3.1 mm dd animal has spine-capped stumps on the disk, which developed from multifid spinules, and broad, dorso-ventrally compressed, rugose arm spines. A 3.7 mm dd specimen has stripes on radial shields resembling the pattern in *O. lineata*. Only the first dorsal arm plate is wide in the 2.3-3.1 mm specimens, but an individual 4.7 mm dd has mostly adult features.

Comparison.—*Ophiothrix stri* is strikingly similar to *O. synoecina* Schoppe, 1996. Both have a somewhat dorso-ventrally compressed body shape, large fairly bare radial shields, smooth, cylindrical basal arm spines projecting over the disk, and other shared morphological, biological and behavioral traits. Among the features distinguishing *O. stri* are a greater number of columns (4-5 vs. 2-3) of interradial stumps, dorsal arm plates lacking a keel, fewer arm spines (maximum of 10 vs. 11), and relatively few stumps on the lateral interradial surface of the disk. Furthermore, the striped arm pattern of *O. stri*, visible throughout the arms of pale-colored individuals and at the arm tips of deeply pigmented individuals, differs from *O. synoecina*, which has a bluish-gray and whitish or reddish disk, arms with whitish, blue and reddish dorsal bands, or uniform bluish-black dorsal coloration, and a purely cream-colored ventral arm surface (Schoppe 1996).

Other Caribbean congeners with which *O. stri* might be confused all share a somewhat dorso-ventrally compressed body shape, and large rather bare radial shields. These include *O. lineata* and *O. cimar*, which also have a dark medial arm stripe set off by pale flanking stripes, and *O. brachyactis*, *O. hartfordi*, *O. platyactis* H. L. Clark, 1939, and *O. lineata* which also have sparse, granulose disk armament. However, rugose, ovoidal, proximally-projecting basal arm spines, and comparatively large, rounded disk stumps distinguish *O. stri*.

Distribution.—At present, known from Cahuita, Costa Rica to Caledonia Bay, Panama, and from the intertidal to a depth of approximately 10 m, generally in less than 3 m.

Biology.—Individuals are cryptic, lethargic, and relatively unresponsive to disturbance. Depending on the locality, they live under coral rubble such as large slabs of *Acropora palmata* or rocks, but in one case were found in clumps of the calcareous alga *Halimeda* sp., and in several instances were found clinging to encrusting sponge. They generally live in elevated structures rather than in proximity to sand or sea-

grass. Individuals beneath rocks cling to the rocks, and do not lie on the sediment. The species is restricted to shallow water, near fringing coral reef. The most densely populated collecting sites were exposed reef platforms, although individuals also occurred on rubble-strewn back reef habitats and in the shallow subtidal. In the San Blas Islands, where the shoreline is sandy, the shallowest individuals were found under slabs of coral rubble at depths to 2 m, and in stands of *Agaricia* and *Porites* spp. at depths to 6 m, on the reef slope.

At Bocas del Toro relatively large numbers of individuals were found at two high-energy hard-bottom localities where the substrate is riddled by the boring echinoid *Echinometra lucunter* (Linnaeus, 1758). Some individuals were found inside the echinoid's burrows, but the association was not obligatory for either species. The ophiuroids were absent from many boreholes, and regularly occurred in rock crevices without echinoids, and under large rocks that sheltered other ophiuroids including *Ophiocoma* and *Ophioderma* species. Relatively few individuals were found at protected localities. Under those conditions other species of *Ophiothrix* predominated in the substrates occupied by *O. stri*, such as at Cahuita where 58 ophiuroids in a sample of the calcareous alga, *Halimeda* spp., were composed of 4 individuals of *O. stri* and 42 *O. angulata*. Similarly, in a sample of coral and rubble collected at a low-energy habitat in the San Blas Islands, 4 *O. stri*, 1 *O. angulata*, and 28 *O. orstedii* Lütken, 1856, were the only ophiuroids found.

The association between *O. stri* and *Echinometra lucunter* seen at Bocas del Toro, Panama was also noted at Puerto Viejo, Costa Rica, but not at Cahuita or Galeta. At the latter two localities its presence in echinoid boreholes may have been overlooked, since exhaustive surveys for the species were not conducted. Furthermore, in at least two instances at Galeta, *O. stri* was found with the nocturnal comatulid crinoid, *Comactinia echinoptera* (Müller, 1840). The ophiuroids were seen in contact with the cirri of crinoids during night dives on the reef slope, at depths of approximately 8 m.

In addition to its biological associations, the coloration of *O. stri* varies within and between localities. Although the species is typically a dark purplish-brown or purplish-gray, yellow individuals were occasionally found in Panama, but not elsewhere. In one instance at Galeta, a large number of yellow individuals were found in the shallow subtidal, under slabs of coral. However, at the same locality individuals collected in the intertidal had such an intense purple coloration that arm stripes were evident only near the tips of the arms. At Bocas del Toro, darkly pigmented individuals prevailed, but some animals were a distinctly pale purplish-gray or ochre. In contrast, the pigmentation of animals at Cahuita was less intense than in the Panamanian animals, and stripes and banding patterning was evident on the full length of their arms. There is also a degree of intraspecific variability in the color of *O. cimar* and *O. synoecina*, but it is not clear if the pigmentation is a genetically determined trait, or under the control of an environmental influence such as diet.

A group of individuals of *O. stri* held in a bowl of standing seawater spawned late in the evening of the day they were collected at Bocas del Toro. The eggs are whitish in color, and each fertilized egg was enclosed in a spacious fertilization envelope. Most of the developing embryos reached a two cell stage several hours after fertilization. Eggs and embryos were readily transported by water movement, but were heavier than seawater. Many adhered tightly to the surface of the glass container, and could be freed only with a strong current of water.

All of the specimens of *O. stri* were examined externally for evidence of brooding, and embryos were not seen in the bursal slits, or in the bursae of dissected females. Of the 15 specimens that were dissected, six were male ($\bar{X} = 6.10$ mm dd, SE = 0.31, range = 4.66-6.78), and 9 were female ($\bar{X} = 7.00$ mm dd, SE = 0.47, range = 4.66-8.65). The overlapping sizes of males and females, and the lack of hermaphroditic specimens, indicates that the species is gonochoric. The eggs in gonads of five of the larger alcohol-preserved females ($\bar{X} =$

9.87 mm dd, SE = 0.32) had a mean diameter of 0.16 mm (SE = 0.002, n = 50, range = 0.11-0.19). However, formalin-preserved eggs that were spawned and fertilized were somewhat larger ($\bar{X} = 0.23$ mm, SE = 0.002, range = 0.21-0.24, n = 30), and were surrounded by a fertilization envelope 30% larger than the egg. The 30% greater diameter of the eggs preserved in formalin than those in alcohol is probably due to the dehydration and shrinkage of the alcoholic material.

DISCUSSION

Distribution and habitat

The westernmost populations of both new species were found at Cahuita National Park in Costa Rica (see Cortés and Risk 1985; Fonseca, 2003 for descriptions of the locality). Populations were also found in western Panama at Bocas del Toro (see Guzmán and Guevara 1998a, b, 1999), from Galeta to Portobello in the central region of Panama (see MacIntyre and Glynn 1976; Cubit et al. 1989), and as far east as the San Blas Islands and at Caledonia Bay near the Colombian border (see Garth 1945; Robertson and Glynn 1977). Despite differences in reef structure among the localities, all the animals were collected on shallow fringing coral reefs exposed to strong currents, large waves, and varying amounts of coastal runoff.

The individuals in Central Panama and the San Blas Islands occupied reef platforms and shallow subtidal slopes. Those at Galeta were abundant intertidally, despite the stress from emersion, heating, wave impact, and predation that cause periodic mass mortality in local echinoid populations (Hendler 1977). At Bocas del Toro they were found near the periphery of the archipelago in relatively high-energy habitats, and at Cahuita they occurred in shallow reef directly behind the outer reef crest. It seems likely that at the mouth of Caledonia Harbor, Panama, they were also found on exposed coastline, based on the information in Garth (1945).

Ophiothrix cimar was relatively more common than *O. stri* in backreef microhabitats, but neither species occurred in nearby lagoonal and mangrove habitats. A possible preference of *O. stri* for high energy sites is borne out by the roughly equal number of both species collected in the backreef at Cahuita, in contrast to the predominance of *O. stri* at the considerably more exposed habitats in Bocas del Toro. Even in the fairly sheltered environment at Cahuita, most individuals were found in less than one meter of water, very close to the forereef crest. At least in certain cases, both species were found in sponge-encrusted microhabitats. Other ophiuroids occurring in close proximity to the new species included common shallow-water Caribbean species such as *Ophiothrix angulata*, *O. orstedii*, *Ophioderma appressum* (Say, 1825), *O. brevicaudum* Lütken, 1856, *O. cinereum* Müller and Troschel, 1842, *O. rubicundum* Lütken, 1856, *Ophiocoma echinata* (Lamarck, 1816), *O. pumila* Lütken, 1859, *O. wendtii* Müller and Troschel, 1842, *Ophioplepis impressa* Lütken, 1859, *Ophiomyxa flaccida* (Say, 1825), *Ophionereis reticulata* (Say, 1825), and *O. olivacea* H. L. Clark, 1901.

Biological associations

The occurrence of *O. stri* in the cavities excavated and occupied by *Echinometra lucunter* is noteworthy, as a similar relationship was previously reported for *O. synoecina* (Schoppe and Werding 1996). The association is not obligatory for *O. stri*, which frequently occurs in crevices without echinoids, and also associates with a crinoid, *Comactinia echinoptera*. Thus, it is likely that the echinoid burrows and crinoid crevices offer a suitable microhabitat for the ophiuroid, but the presence of *O. stri* together with echinoids and crinoids is incidental. The association of *O. stri* and *E. lucunter* was observed in Bocas del Toro, Panama and Puerto Viejo, Costa Rica, and the association with *C. echinoptera* was seen at Galeta, but not at other localities where the species co-occurred. However, extensive surveys were not carried out to assess the habitat preferences and requirements of *O. stri*.

In contrast with *O. stri*, *O. synoecina* was described as an obligate associate of *E. lucunter* (Schoppe 1996; Schoppe and Werding 1996). At the study site in Colombia, where large numbers of *Echinometra* riddled the reef substrate, up to 95% of the boreholes were occupied by *O. synoecina*, and up to 10 ophiuroids were found per borehole, reportedly nestled beneath the echinoid. Schoppe and Werding (1996) also indicated that the Colombian echinoids do not leave their cavities, which is surprising since that is not the case elsewhere in the Caribbean (Hendler et al. 1995). Although observations on *O. synoecina* led to the conclusion that it is "found exclusively in association with *Echinometra*" (Schoppe and Werding 1996:184), it is not clear whether the ophiuroid was entirely absent from other substrates. That point should be re-evaluated, since the observations on *O. stri* suggest that *O. synoecina* may be less host-specific than has been suggested.

The observation that *O. stri* and *O. cimar* may live in sponge-encrusted niches is of interest, considering the habits of *O. lineata*. The latter species is an obligate symbiont on tube sponges. It occurs on sponges with *Ophiothrix angulata* and *O. orstedii*. However, it has not been found in association with *O. cimar* or *O. stri*, despite its close morphological similarities, particularly to the latter species. The nature of the relationship of the new species with encrusting sponges is yet to be determined, and more extensive, detailed observations on their associations are desirable.

Reproductive biology

Two Caribbean *Ophiothrix* species are known to have planktotrophic larvae, *O. angulata* and *Ophiothrix suensonii* Lütken, 1856. They have small oocytes that are 0.10–0.13 mm in diameter, and only slightly smaller than the fertilization envelope. *Ophiothrix suensonii* develops from an 8-armed ophiopluteus larva, which is typical of the ophiotrichids that have been reared (Stancyk 1973; Mladenov 1985). In contrast, *O. orstedii*, another Caribbean species, produces eggs 0.25 mm diameter, enclosed in a very spacious fertilization envelope.

lope, and has a rapidly developing, 2-armed larva (Mladenov 1979). Although it is the only ophiotrichid known to have abbreviated development, lecithotrophic larvae are the norm for ophiuroid species with moderately yolky eggs (Hendler 1991).

The three Caribbean *Ophiothrix* species with known development have adults with separate sexes, and although their eggs are heavier than seawater they are readily suspended because the fertilization envelope is not adhesive. They differ markedly from *O. synoecina*, which is protandric, with a small male, and a transitional stage with ovotestes that develops into a large female, which is thought to brood embryos externally (Schoppe and Holl 1994). Its large yolky eggs, up to 0.30 mm in diameter, are reportedly carried in "clusters...in front of the mouth" of females, and the young ophiuroids were described as clinging to the females for two weeks (Schoppe and Holl 1994:472). Its combination of reproductive traits is unusual, as *O. synoecina* is the only protandric ophiotrichid that is known, and only the second ophiuroid species that is suggested to brood externally; the embryos of other brooding ophiuroids develop in the parent's bursae. The expression of protandry in the species is of additional significance since, among the ophiuroids, hermaphroditism has only been observed in brooding species (Hendler 1991). In regard to the issue of brooding in Caribbean *Ophiothrix* species, it is notable that there are minute, juvenile ophiuroids clinging to the very small type specimens of *O. brachyactis* and *O. hartfordi*. It remains to be determined if the association is indicative of external or internal brooding reproduction or was coincidental.

Schoppe and Holl (1994) did not describe how the eggs of *O. synoecina* come to aggregate in "clusters" and how they are held by the females. If the eggs of *O. synoecina* have an adhesive fertilization envelope, like those of *O. stri*, it is possible that they could stick to one another or to the female, facilitating their manipulation by the female. The eggs of *O. stri*, however, did not form clusters, nor were they gathered or clasped by the adult individuals. Although

conditions in vitro were substantially different than under natural conditions, the laboratory observations suggest that were *O. stri* to spawn in a semi-enclosed space, like an *Echinometra* burrow, its fertilized eggs would not be "carried" by the females, although they could adhere to the walls of the cavity and develop near adult ophiuroids. Thus, there are similarities in the reproductive behaviors of *O. synoecina* and *O. stri* in terms of their yolky eggs and demersal development, however the latter species is gonochoric and does not appear to brood or to carry associated juveniles.

Systematic affinities

There are similarities between *O. lineata* and members of the subgenus *Placophiothrix* that may have significance for the classification of the new species. A. M. Clark (1966) restricted the genus *Placophiothrix* H. L. Clark, 1938 to subgeneric rank, because the distinctions among *Placophiothrix* and the other ophiotrichid subgenera were, and remain, elusive (Hoggett 1991). She characterized *Placophiothrix* by arms usually 6-9 times the dd, radial shields bare or with few stumps, moderately large disk scales bearing spaced spines, spinelets, or stumps, and opaque arm spines (Clark and Rowe 1971). Despite the resemblance of *O. lineata* to the *Placophiothrix* species, all of which are Indo-West Pacific, A. M. Clark (1966) referred the Caribbean species to the subgenus *Ophiothrix*.

Ophiothrix stri shares a number of important features with *O. lineata* including: large, separated radial shields bearing few stumps, granulose disk armament almost entirely restricted to the dorsal surface, borne on moderately large scales; wide, flat, hexagonal dorsal arm plates, broadly in contact; slotted first ventral arm plate and overlapping 2nd and 3rd ventral arm plates; broad, octagonal ventral arm plate; dorso-ventrally compressed, rugose lateral arm spines; striped arms. They also differ in important respects, particularly the more elongated, slender compressed basal arm spines, and smaller, multiple stumps on the disk scales of *O. lineata*. However, *O. stri* is most similar to *O. synoecina*, the only note-

worthy differences being in the shape and microstructure of the dorsal arm plate, proximity of the 2nd and 3rd ventral arm plates, structure of the lowest arm spine, and superficial differences in pigmentation. The three species resemble each other, considerably more than they resemble *O. cimar*, but have in common with the latter: disk armament borne on moderately large scales, wide dorsal arm plates, rugose, compressed arm spines, slotted 1st ventral arm plate, and long, narrow 2nd ventral arm plate overlapping the 3rd ventral arm plate. They resemble to a lesser degree several small, poorly studied Caribbean congeners with broad dorsal arm plates and small disk stumps, *Ophiothrix brachyactis*, *Ophiothrix hartfordi*, and *Ophiothrix platyactis*. The latter three species are represented in museums by only a few, small specimens, which might in fact be immature individuals. Each differs in a significant way from *O. cimar*, *O. stri*, *O. synoecina*, and *O. lineata*. In addition to considerable differences in arm spine morphology, and the prevalence of multiple stumps on disk scales, *O. platyactis* has a scaled ventral interradius, *O. brachyactis* has square ventral arm plates, and *O. hartfordi* has relatively large scales at the center of the disk.

The eggs of *O. stri* and *O. cimar* are approximately 0.16 mm diameter, slightly smaller than those of *O. lineata* ($\bar{X} = 0.19$ mm, SE = 0.002, n = 50). The egg size of the latter species was estimated from measurements of oocytes in the gonads of alcohol-preserved females ($\bar{X} = 11.76$ mm dd, SE = 1.09, n = 5), as were the size of *O. cimar* and *O. stri* eggs. However, the larger size of formalin preserved oocytes of *O. stri* suggests that all three species have egg diameters somewhat in excess of 0.2 mm. In any case, they fall within the size range (0.13-0.35 mm diameter) of eggs produced by ophiuroids that have abbreviated development (Hendler 1991).

Even if *O. lineata* and similar species are related to *Placophiothrix*, the characteristics of their eggs sets them apart from *Ophiothrix spongicola* Stimpson, 1855, the only member of *Placophiothrix* whose development has been studied (Selvakumaraswamy and Byrne 2000). Its eggs are

small, about 0.13 mm in diameter, and give rise to a planktotrophic, 8-armed ophiopluteus. The morphological similarities among the first four species suggest that lecithotrophy is expressed in members of one, or possibly two clades of Caribbean Ophiotrichidae. The particularly close similarity between *O. stri* and *O. synoecina* suggests that they are sister species, probably with a common ancestor that was a gonochoric broadcast-spawner, and they appear to have a greater systematic affinity to *O. lineata* than to *O. cimar*. Furthermore, those four species are considerably more similar to one another than to *O. orstedii*, which also has lecithotrophic development, but has a radically different dorsal arm plate, 1st ventral arm plate, and spine morphology. A phylogenetic analysis of use in evaluating those hypotheses might also clarify the evolutionary connection between hermaphroditism and brooding, particularly if the full range of Caribbean *Ophiothrix* could be considered. At present, carrying out the analysis would be a daunting challenge, since several key species are known only from one or two, old, dried type specimens, and it is likely that other species still remain to be described.

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